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INTERSEXUALITY IN DROSOPHILA VIRILIS AND ITS BEARING ON SEX DETERMINATION

By G. A. Lebbdeff

Department of Plant Breeding, Cornell University

Communicated March 14, 1938

It is a well-established fact that in higher animals and plants individuals of either sex possess both female and male tendencies. The superiority of the one tendency over the other determines the sex.

There are two principal theories as to the balance between sex tendencies: qualitative of Bridges, and quantitative of Goldschmidt. These two theories have been subjected to criticism and to some modification. A review of the literature and the bibliography will be given in a detailed account of this work to be published later. For the present it is sufficient to mention two shortcomings of these theories.

1. In the experiments noted no sex gene has been isolated, and therefore the balance between female and male tendencies has been studied only indirectly.

2. In these studies, the female and male tendencies have been considered as alternative, and therefore these theories do not explain the nature of hermaphroditism.

The present author for the last several years has been engaged in the study of intersexuality in *Drosophila virilis*. In the course of this study facts concerning sex expression in this species have been discovered which throw new light on the mechanism of sex determination. The hypothesis here presented is the result of these studies. The progress of this work has been reported before meetings of the Genetics Society of America (Lebedeff, 1934 and 1938). The author wishes to express his sincere appreciation to Professors R. A. Emerson and L. W. Sharp of Cornell University for their advice and criticism.

Several years ago in one of the *D. virilis* stocks a new mutant was discovered. The gene concerned was called intersex (*ix*)* and was found to be located in the third chromosome, the exact locus being determined. The gene has no effect on males, but females homozygous ix^m/ix^m become converted into males which are sterile. In the course of this work two

modifying genes (designated *A* and *B*) have been found which delay the transformation of these females into males, thereby bringing about the development of hermaphrodites. The genetical evidence indicates that the number of intersex modifying genes is probably greater than two and that their effect is cumulative. The degree of hermaphroditism varies from female-like to nearly male-like. The specimens intermediate between these two extremes possess well-developed female and male sexual characteristics, including external and internal sexual organs and gonads. However, they are sterile, since gametogenesis is abortive.

Genetical and morphological studies of these intersexes, supplemented by embryological studies of gonads, indicate that the Time Law of Intersexuality found to be responsible for intersexuality in Lymantria and *Drosophila melanogaster* applies to *D. virilis* intersexes also. The intersexes of *D. virilis* start to develop as females and then from a certain stage, known as the turning point, proceed to develop in a male direction. The sexual organs whose imaginal discs are differentiated before the turning point is reached develop into female organs. On the other hand, the imaginal discs which appear after the occurrence of the turning point develop in the adult intersex into male organs. Thus, in *D. virilis*, as in the other species mentioned, the time of the reversal determines the degree of intersexuality. Nevertheless, intersexes of *D. virilis* differ morphologically from all other types, being essentially hermaphrodites because of the peculiarity in the development of those organs whose imaginal discs had not become fully differentiated at the time of reversal. Such imaginal discs develop into female organs, but along with them male organs appear, presumably from fresh outpushings. The two systems, the original female and the additional male, develop side by side, resulting in hermaphroditism.

The study of the development of gonads in these intersexes indicates that in all morphological types of intersexes the gonads start their development as ovaries. In the female type of intersexes the ovaries continue their development, though it is retarded in various degrees. In the hermaphrodites, after the occurrence of the "turning point" the female germinal cells in the ovaries are gradually transformed into male-like ones, while the ovary buds out a testis-like structure to which migrate some of the oocytes, now transformed into spermatocyte-like cells. In the male type of intersexes the ovaries are gradually transformed into testis-like organs, in which the cells undergo a process of transformation into spermatocyte-like cells, most of which eventually disintegrate.

These findings are of primary theoretical importance. According to the prevalent theories, the development of an individual at any given time is under the control of either the male or the female tendency, depending on the quantitative or qualitative balance between the two. These two

tendencies are considered as alternative. Although this assumption is obviously contradictory to the state of hermaphroditism, it has been retained in most theories, because our understanding of hermaphroditism was entirely unsatisfactory. "Our present conception of hermaphroditism is the most unsatisfactory chapter in the whole sex problem, and our material is insufficient to permit of a correct genetic or physiological understanding." (Goldschmidt, 1923). However, our own studies indicate that the development of an individual can proceed under the direct and partially simultaneous influence of tendencies of both sexes, resulting in the development of hermaphrodites. It is hoped that the problem discussed here may improve our understanding of the genetics and the physiology of hermaphroditism.

We are now prepared to ask what is the bearing of this study on the mechanism of sex determination? To answer this question we should first clarify our concept of the ix^m gene and its normal allele.

Goldschmidt (1935) and Patterson, Stone and Bedichek (1937) ventured to deal with these questions. Their conclusions were based on the preliminary report of our work (Lebedeff, 1934). Goldschmidt considers the ix^m gene as an autosomal male determiner, the potency of which is not strong enough to overbalance the female tendencies of the 2X:2A mechanism. The ix^m gene is compared to weak *M* of Lymantria. Patterson and his co-workers also considered the ix^m gene as a gene for maleness. But its normal allele is considered to be the gene for femaleness.

Our experimental data, especially those unknown to the above mentioned authors, indicate that these concepts of the ix^m gene and its normal allele are incorrect. According to our conception, the normal allele of the ix^m gene is a normal male determiner (Ix^m), and in the 2X:2A individuals it is in a balanced condition. The mutant ix^m is considered to be a strong allele of Ix^m. The potency of this gene is so great that it partially overrides the 2X:2A mechanism, resulting in the conversion of females homozygous for this gene into males which are sterile. The discovery of this gene is considered by Patterson and his co-workers as the nearest approach to a demonstration of the action of a single gene in sex determination in Drosophila. To this we may add that this discovery permits for the first time a more direct approach to the rôle of a balance between female and male determining genes in the process of sex determination.

It is a well-established fact that in Drosophila the X chromosome is the carrier of the gene (or genes) for femaleness. Without going into a detailed discussion of this question, which has aroused controversy in the last few years, we may assume, probably to the satisfaction of a large group of geneticists, that the theory of a single female gene in the X chromosome in Drosophila is the more probable. Accordingly, the normal Drosophila females are homozygous for this gene (*FF*), and the males

have a single dose of it (F). To this genotype we shall now add the gene for maleness (Ix^m) located in the third chromosome of *D. virilis*. The normal females then will be $FF\ Ix^m\ Ix^m$ and the normal males $F\ Ix^m\ Ix^m$.

It is a simple matter to explain why $F\ Ix^m\ Ix^m$ animals develop into normal males, assuming that two doses of Ix^m are more potent than one dose of F. But it is not so easy to explain why $FF\ Ix^m\ Ix^m$ individuals develop into normal females. According to Goldschmidt's theory, the quantitative difference between F and M shifts the balance into one or another direction. According to our hypothesis both M and F factors are equally potent in determining whether the animal shall develop into a female or a male, but there is a special mechanism which decides which of these factors will function in the zygote. This mechanism either inhibits the activity of the F factor, thus giving to the M factor full control in determining sex, with the consequent development of normal males; or the mechanism inhibits the activity of the M factor, thus shifting the control of sex development to the F factor, resulting in the development of normal females.

TABLE 1

Phenotypical expression of the 2X:2A individuals in regard to the ix^m gene with its modifiers and suppressors. To simplify the scheme suppressors (S_3 and S) and modifier (B) are used in a heterozygous condition only. For the same reason only one modifier is considered here.

Any one of these genotypes when in a 1X:2A individual results in the development of normal males.

We have found such a mechanism in *D. virilis*. Two dominant suppressors were found, either one of which entirely inhibits the action of the ix^m gene (table 1). Therefore, 2X:2A individuals homozygous for ix^m and homo- or heterozygous for both or either of these suppressors are not converted into sterile males but develop into normal females. One of these suppressors, designated as S_3, is located in the third chromosome, and therefore is linked wth ix^m and its normal allele Ix^m. The other suppressor, designated as S, belongs to one of the other autosomes. These suppressors probably are not sex genes, and are considered as neutral. However, they play an important rôle in the mechanism of sex determination in that they can inhibit the action of Ix^m, thus determining the direction in which the development will proceed.

Now we shall add these suppressors to the above outlined formulae for male and female. The FF ($Ix^m\ Ix^m\ S_3S_3$) SS is a female because the development of the male tendency is inhibited by S_3 and S suppressors. The F ($Ix^m\ Ix^m\ S_3S_3$) SS individuals develop into males in spite of the presence of both suppressors of maleness, because two doses of Ix^m are opposed by only one dose of F. Under such conditions the suppressors

are unable to inhibit completely the action of Ix^m, hence, the balance goes in a male direction.

To evaluate further the nature of the ix^m gene and its suppressors let us make one assumption, namely, that male-like intersexes (which often resemble normal males in all features) might become fertile. This might result either from a mutation of the ix^m gene into its stronger allele, or from the appearance of a new mutant, a specifically female suppressor (S_f). In the former case it would probably result in a mechanism comparable to that of Lymantria, and in the latter case it would lead to the establishment of the WZ mechanism of sex determination. Then the cross between an $ix^m/+$ female and an ix^m/ix^m male-like intersex would result in a female and male population in a ratio of 1:1. But both females and males from this cross would be of 2X:2A constitution. Thus, a new race of *D. virilis* would be established in which the XY mechanism is displaced by the WZ, since females would be heterozygous and males homozygous for the sex chromosome. The third chromosome, in which the ix^m gene is located, would have assumed the rôle of the sex chromosome. The males in this hypothetical case would be genotypically $FF\ ix^m\ ix^m\ S_f\ S_f$ and the females $FF\ Ix^m\ ix^m\ S_f\ S_f$ in constitution. In this case F is homozygous in both sexes, and ix^m is homozygous in males and heterozygous in females, and S_f suppresses F activity in individuals homozygous for both F and ix^m factors.

Thus, XY and WZ mechanisms are visualized as the factors controlling the activity of the suppressors. In the Drosophila XY type the suppressors inhibit the activity of the M gene, and for that reason FF ($MM\ S_3S_3$) SS animals develop into females. In species with the WZ mechanism suppressors inhibit the female tendency, both sexes probably being homozygous for FF. In unisexual species in which neither the XY nor the WZ mechanism is known, the effectiveness of suppressors is probably influenced by the heterozygosity of either F or M factors. This condition is less balanced, the specificity of the suppressors may be undifferentiated and the development may proceed under the influence of both F and M genes, resulting in hermaphroditism. In bisexual species all individuals are assumed to be homozygous for both F and M factors, and therefore suppressors are not effective.

It is evident from the data here presented that hermaphroditism may occur only in the sex homozygous for both F and M factors. In species with the XY mechanism hermaphrodites develop when the M factor mutates to its stronger allele, as has been demonstrated in our studies. In the species with the WZ mechanism hermaphrodites probably will develop when the F factor mutates to a stronger allele. In the species in which there is no sex chromosome both sexes are homozygous for both F and M factors and hermaphroditism is therefore of common occurrence.

The experiments here briefly described are essentially a genetical and physiological study of the sex determining mechanism in Drosophila in the process of transformation of a normal unisexual into a hermaphroditic (though non-functional) state. In connection with this study the experiments of Emerson (1932) and Jones (1934) with maize are of considerable interest. These authors independently described the genetics of the transformation of normal monoecism into dioecism.

Normally, maize plants are monoecious, the terminal inflorescence bearing staminate and the lateral bearing pistillate flowers. In the inflorescence of each sex, rudiments of the opposite sex are usually present. Numerous genes, mostly recessive, have been found which influence the expression of sex. These genes are assumed to stimulate a certain potentiality that is usually dormant, and suppress the other character normally functioning. By a suitable combination of these genes strains were obtained which produced only a pistillate or a staminate inflorescence. These genes are considered as a few of numerous sex genes, the interaction of which is responsible for monoecism in this species.

Our experiments with *D. virilis* hermaphrodites permit a further evaluation of this work. According to our hypothesis, in monoecious species both sexes are homozygous for both *M* and *F* factors, and therefore are free of specifically *M* or *F* suppressors. There is, however, some mechanism, which was also assumed by Jones, for the strict localization of flowers of both sexes on different parts of the plant. In maize, staminate flowers occupy the terminal position, and pistillate flowers the lateral position.

All known genes in this species, which affect flower expression, can be classified into several groups according to the effect they produce. Some of them inhibit the development of the staminate flowers in their normal terminal position. They are assumed to be male (*M*) suppressors. To this group belong numerous so-called male-sterile mutants. While the genes which inhibit the development of the pistillate flowers in their normal lateral position are assumed to be female (*F*) suppressors, to which such mutants as barren-stalks and silkless belong.

Besides these suppressors, which inhibit the development of either male or female flowers in their respective normal position on the plant, there are a number of genes which stimulate the development of male or female flowers in places where they are usually in a very rudimentary state. These genes are assumed to be male (*M*) or female (*F*) stimulating genes, or male and female "exciters" (Aida's terminology). The development of usually dormant stamens in the lateral inflorescence is assumed to be due to male exciting genes, to which such mutants as dwarfs and anther ear belong; while the development of usually dormant pistils in the terminal inflorescence is assumed to be a result of female exciters, to which such mutants as tassel-seed 4 and 5, and silky ears belong.

Several known mutants in maize seem to have a double effect, possibly due to the fact that two or more genes are closely linked. To this series belong such mutants as tassel-seed 1, 2 and 3, which are both male suppressors and female exciters.

In our discussion of the mechanism of sex determination the rôle played by the sex modifying genes has not been touched. The presence of these genes can be detected only in the intersexes. Bridges (1932) and Dobzhansky and Schultz (1934) have demonstrated that the female sex modifying genes in *D. melanogaster* are preponderantly located in the X chromosome. In this study two such genes have been demonstrated in *D. virilis*. The available evidence indicates that the number of such genes is probably greater than two and that their effect is cumulative. Their function is to fix the time of the turning point, i.e., to determine the extent of the development of one sex before the control of development is shifted to give the opposite sex. The activity of these genes can be easily influenced by internal and external environment.

It is clear that the sex modifying genes (which properly should be called intersex modifying genes) play an important rôle in the development of a given sex. Recently much attention has been given to the question of the rôle played by these genes in the sex determining mechanism. The Pasadena group of geneticists led by Bridges, Dobzhansky and Schultz, consider these genes as the sex determining genes. Their opponents, Goldschmidt, Patterson and co-workers consider that the presence of these genes has not been sufficiently demonstrated.

The present author is inclined to take an intermediate position in this discussion. The presence of the intersex modifying genes cannot be disputed, but the rôle played by them in the development of normal males and females is debatable. As intersex modifying genes they are involved in the development of sex. But in the complex development of a given sex two processes can be recognized: sex determination and sex differentiation (Baltzer, Goldschmidt, Witschi). The so-called sex modifying (or intersex modifying) genes, according to our hypothesis, are the sex differentiating genes.

Ascribing to intersex modifying genes the rôle of sex differentiation, we naturally should provide an explanation of triploid intersexuality, in connection with which these genes were first detected. According to our hypothesis, triploid intersexes of *D. melanogaster* are of *FF* (Ix^m Ix^m Ix^m $S_3S_3S_3$) *SSS* constitution. It is obvious that the initial balance is on the male side, so that these individuals should start their development as males. The balance, however, is not stable and intersexuality results. It is also possible on the basis of our study to explain why haploid Drosophila *F* (*M* S_3) *S* is a female.

Our conception of the mechanism of sex determination and differentia-

tion in *D. virilis* may be summarized as follows. Sex in this species is determined by the balance between the gene for femaleness (*F*) located in the X chromosome, and the gene for maleness (Ix^m) located in the third chromosome. These factors are equally potent in determining whether the animal will develop into a female or a male. The balance between these genes is maintained by a set of suppressors, which inhibit the activity of the Ix^m gene when it is opposed by an equal dose of *F* genes. For that reason *FF* (Ix^m Ix^m S_3S_3) *SS* individuals develop into females. The *F* (Ix^m Ix^m S_3S_3) *SS* individuals develop into males in spite of the presence of the Ix^m suppressors, because the Ix^m factors are not counterbalanced by an equal dose of the *F* factors. The XY mechanism is visualized as the factor controlling the activity of the suppressors, which are specifically suppressors of maleness.

The conception outlined here is not considered final. It is hoped that further research with *D. virilis* intersexes and with the sex genes of maize will help in evaluating the hypothesis here outlined.

$\frac{ix^m\ S_3}{ix^m\ +}$ $S/+$ $B/+$ female

$\frac{ix^m\ S_3}{ix^m\ +}$ $S/+$ $+/+$ female

$\frac{ix^m\ S_3}{ix^m\ +}$ $+/+$ $B/+$ female

$\frac{ix^m\ S_3}{ix^m\ +}$ $+/+$ $+/+$ female

$\frac{ix^m\ +}{ix^m\ +}$ $S/+$ $B/+$ female

$\frac{ix^m\ +}{ix^m\ +}$ $S/+$ $+/+$ female

$\frac{ix^m\ +}{ix^m\ +}$ $+/+$ $B/+$ hermaphrodite

$\frac{ix^m\ +}{ix^m\ +}$ $+/+$ $+/+$ sterile male

* The gene was called intersex (*ix*) soon after it had been discovered, and before its nature had been studied. Now we know that this gene is the gene for maleness, and therefore it will be called ix^m and its normal allele Ix^m.

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*THE SEDIMENTATION CONSTANT OF VISUAL PURPLE**

BY SELIG HECHT AND E. G. PICKELS

LABORATORY OF BIOPHYSICS, COLUMBIA UNIVERSITY, AND LABORATORIES OF THE INTERNATIONAL HEALTH DIVISION, ROCKEFELLER FOUNDATION, NEW YORK

Communicated March 9, 1938

1. Visual purple, the photosensitive substance of the vertebrate rods, is most likely a protein of high molecular weight.[1] We have determined its sedimentation constant under several conditions in order to answer some questions with regard to its absorption spectrum, its size and chemistry.

For this purpose, measurements of its sedimentation rate were made according to Svedberg's procedure,[2] but using the air-driven ultracentrifuge of Bauer and Pickels.[3]

The two certain criteria of visual purple are its color as determined by its absorption spectrum in the visible region of the spectrum, and its capacity to be bleached by visible light. The absorption spectrum of visual purple in the visible region is an approximately symmetrical band[4] with a maximum at 500 mμ. While there may be some doubt that all of the absorption on the short-wave side of this maximum is due to visual purple alone and not to contaminating substances, it is certain that the absorption on the long-wave side is due solely to visual purple, since this absorption disappears almost completely after visual purple has been bleached. Therefore, the sedimenting visual purple was photographed with light from the mercury green line 546.1 mμ which falls in the middle of the long-wave side of the absorption spectrum of visual purple.

The light used in photographing the solution did not perceptibly bleach it because the exposures were quite short. However, care had to be taken to shield the sample from extraneous light while preparing it for centrifugation. The filling of the cell, and its location in the rotor were done in a dark room by dim red light; above and below the cell, the openings in the rotor were carefully closed with rubber stoppers, which were removed in the dimly lighted centrifuge room only at the very last moment, just as the rotor was placed in the complete darkness of the vacuum chamber which houses it during operation.

2. The sedimentation velocity of frog's visual purple was measured in each of four samples prepared[5] as already described and buffered at pH 7.7. In each instance, the speed was 46,800 r. p. m. and the mean centrifugal force 160,000 times gravity. The concentration of each solution was 20 retinas per cc. For convenience the preparations may be referred to as *A*, *B*, *C* and *D*, the order being that in which they were made over a period of five weeks. The photographs and their microphotometer tracings showed only one sedimenting boundary in each experiment. Three of the preparations (*A*, *C*, *D*) were consistent in their behavior while one (*B*) was slightly different. Each solution was stored near 0°C. after preparation and was never more than a day or two old when used for centrifugation. Solutions which are months or years old show differences which are not now understood.

The sedimentation constant, S_{w20}, of a substance as defined by Svedberg[2] expresses its rate of sedimentation under a set of standard conditions, i.e., in a suspending medium having the density and viscosity of water at 20°C. For its computation from the measured sedimentation rate, there must be known the density and the viscosity of the experimental medium. Determinations of these two quantities were made at different temperatures

on the digitonin-buffer solution used for extracting the visual purple from the retinas. At 20°C., the density was 1.032, and the viscosity 1.058×10^{-2} dyne-sec. per square cm.

The values of the sedimentation constant for preparations *A*, *B*, *C* and *D* turn out to be 11.4, 10.7, 11.2 and 11.1×10^{-13} cm. per dyne per sec., respectively. These give an average value of 11.1×10^{-13} cm. per dyne per sec., from which even the extreme (*B*) deviates by less than 4 per cent. This value of S_{w20} is of the same order of magnitude as those found[2] for such proteins as edestin, excelsin and phycoerythrin, and leaves no doubt about the fact that visual purple is a relatively large molecule.

3. The absorption spectrum of even the best preparations of visual purple is not quite symmetrical in the visible spectrum; it is distinctly higher on the short-wave side, and the degree of this asymmetry varies with the method of preparation.[4] With the preparations here used the asymmetry is at a minimum, though it is still present. To determine whether this persistent asymmetry is real or whether it is due to other substances present in the solution, we measured the rate of sedimentation of preparations *C* and *D*, using the mercury blue line 435.8 mμ for photographing the cell. In fact, we so arranged the work that in each experiment these photographs were made alternately with the preceding ones on the same sample that was being centrifuged.

The results show clearly that the asymmetry of the absorption spectrum is an integral property of visual purple because only one boundary was apparent, and the sedimentation constant is the same as that measured with the green line. The respective values of S_{w20} are 11.0, and 11.2×10^{-13} cm. per dyne per sec. and are experimentally indistinguishable from the previous values, the two averages being identical.

4. To determine whether visual purple shows any changes on bleaching, detectable by this method, each of three solutions was bleached at room temperature and kept near a north window for several hours so that all the changes associated with bleaching would be over. Each sample was then centrifuged in the usual way.

Preparation *D* was measured with green and with blue light. The photographs with the green line showed almost no trace of a boundary, thus confirming the notion that the absorption in the green region is due entirely to unbleached molecules. The photographs with the blue line were much like those of the original unbleached solution, and gave a sedimentation constant of 11.3×10^{-13} cm. per dyne per sec. which is experimentally the same as that of the unbleached material. Preparation *A* (bleached) was photographed with ultra-violet light and gave a value of $S_{w20} = 11.2 \times 10^{-13}$. This particular preparation seemed more pure than usual because the measurements of sedimentation rate from photographs taken in the ultra-violet and visible regions are identical. Prepa-

ration B again gave slightly aberrant results. The bleached solution measured with blue light yielded an S_{w20} value of 10.3×10^{-13} while with ultra-violet $S_{w20} = 9.7 \times 10^{-13}$. The unbleached solution measured in the ultra-violet gave $S_{w20} = 10.1 \times 10^{-13}$. Very likely, preparation B was not as pure as the other three, because the ultra-violet photographs for the unbleached and bleached solutions showed not only the usual boundary but a pronounced density gradient throughout the solution, indicating the presence of some light-absorbing materials having widely different separation rates.

These measurements show that the bleaching of visual purple in solution does not represent any drastic splitting of the molecule; the evidence is compatible with the notion that the bond between the carotenoid portion and the protein portion of the molecule is either rearranged or perhaps broken by light,[7] but it does not establish either of these ideas.

5. The molecular weight of a protein may be computed from the measured values of its diffusion and sedimentation constants. The diffusion coefficient of visual purple has already been determined[1] in digitonin-buffer solutions at 6°C. The value found under these conditions, $D_6 = 2.2 \times 10^{-7}$ sq. cm./sec., becomes $D_{w20} = 3.5 \times 10^{-7}$ sq. cm./sec. when referred to the standard conditions defining the diffusion constant. However, several days were necessary for carrying out the measurements on which this value is based, and some of the solutions contained a good deal of neutral salt. The value secured may therefore be a little low because visual purple solutions show a tendency toward slow aggregation. This is evidenced by the fact that old solutions, though clear and normally colored, sediment more rapidly than those freshly prepared.

The existence of aggregates is further supported by determinations of the diffusion constant made from the blurred boundaries of the sedimentation photographs. The variations of concentration through the boundaries were not strictly in accord with those attributable to a normal diffusion of single molecules,[2] indicating some inhomogeneity in the separating particles. There was distinct evidence of some visual purple particles moving slightly faster, in varying degree, than the principal component. The diffusion constant D_{w20} for the principal component secured from the boundaries of sedimentation photographs ranged from 4.5×10^{-7} to 7×10^{-7} sq. cm./sec., the lower values corresponding to measurements taken from the early stages of centrifugation before the inhomogeneities of sedimentation had become accentuated. These lower values are near enough those previously determined to suggest a probably correct value for D_{w20} of 4×10^{-7} sq. cm./sec.

From this diffusion constant and the sedimentation constant, the molecular weight may be computed in terms of Svedberg's well-known equation. The molecular weight of visual purple comes out as 270,000 pro-

vided the molecules have a density equal to that of most proteins, i.e., 1.33 gm./cc. This value of the molecular weight is about one-third of that secured from the diffusion constant alone as previously measured by the method of Anson and Northrop.[6,7] The difference in the results from the two methods is not unexpected and has been found for other proteins.

The molecular weight may, of course, be computed from the sedimentation constant alone, without use of the diffusion coefficient, provided it is assumed that the molecules are spherical. Applying Stokes's law, the radius of the molecule may be calculated, and if the density is assumed to be 1.33 as before, the molecular weight becomes 200,000. This represents a minimum value, since the spherical form is most favorable for rapid sedimentation. The fair agreement between the two values secured from the sedimentation constant with and without the diffusion constant indicates a shape for the visual purple molecule which is probably not greatly different from that of a slightly oval particle.

* Aided by a grant from the Rockefeller Foundation to Selig Hecht.

[1] S. Hecht, A. M. Chase and S. Shlaer, *Science*, **85**, 567 (1937).

[2] T. Svedberg, *Chem. Reviews*, **20**, 81 (1937).

[3] J. H. Bauer and E. G. Pickels, *Jour. Exptl. Med.*, **65**, 565 (1937).

[4] E. Koettgen and G. Abelsdorff, *Zeit. Psychol. Physiol. Sinnesorg.*, **12**, 161 (1896); G. Wald, *Nature*, **139**, 587 (1937); R. J. Lythgoe, *Jour. Physiol.*, **89**, 331 (1937); A. M. Chase, *Jour. Gen. Physiol.*, **21** (1938).

[5] Dr. Aurin M. Chase kindly made these extractions for us.

[6] M. L. Anson and J. H. Northrop, *Jour. Gen. Physiol.*, **20**, 575 (1937).

[7] G. Wald, *Jour. Gen. Physiol.*, **19**, 351 (1935).

BIOLOGICAL DIFFERENCES IN THE ACTION OF SYNTHETIC MALE HORMONES ON THE DIFFERENTIATION OF SEX IN THE CHICK EMBRYO

BY B. H. WILLIER, MARY E. RAWLES AND F. C. KOCH

DEPARTMENT OF ZOÖLOGY, UNIVERSITY OF ROCHESTER AND DEPARTMENT OF BIOCHEMISTRY, UNIVERSITY OF CHICAGO

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In a former investigation[1,2] it was shown that male hormone preparations obtained from male human urine and bull testis act differently upon the developing gonads and gonoducts of the chick embryo. The urinary preparations brought about a feminization of the genetic males just as oestrone and oestriol did. Also they had a masculinizing effect as was shown by (1) the hypertrophy of the potential vasa deferentia (Wolffian ducts) in embryos of both sexes and (2) the inhibition of the oviducts in

genetic females. The bull testis preparations, on the contrary, in the concentrations used produced no changes except an hypertrophy of the Wolffian ducts in both sexes. These biological differences in action were ascribed tentatively to the presence of androsterone and dehydroandrosterone in the urinary preparation and of testosterone in the bull testis preparation.

The purpose of the present paper is to analyze the effects of the synthetic male sex hormones giving particular attention to the biological differences in their action. Either propylene glycol or sesame oil solutions of androsterone, dehydroandrosterone, androstenedione and testosterone propionate were introduced into eggs incubated from 43 to 72 hours, stages either prior to or during the early formation of the gonad primordium. The dosage was single and ranged from 0.02 to 2.4 mgs. Development was then continued until the 16th, 17th or 18th day. The hormones were administered to 300 eggs. Of those treated with androsterone and dehydroandrosterone 34% survived, whereas with testosterone propionate 74% survived, thus indicating a considerable difference in the toxicity of the androgenic substances used. The sex ratio of the surviving embryos is 54 ♀♀ : 64 ♂♂, showing no differential effect. All survivors were examined for changes in the gross anatomy of the gonads and gonoducts. The histology of the gonads and portions of the gonoducts was studied in 76 cases. By using F_1 embryos of the cross Barred Rock ♀ × Rhode Island Red ♂, the original sex was readily ascertained by differences in sex-linked plumage characters.

Genetic Females.—Each of the hormones, except androstenedione which is ineffective in the concentration used (0.09–0.66 mg.), brings about a modification in the form and structure of the gonads and gonoducts of the genetic females (Figs. 2, 4 and 5). Usually with concentrations less than 1.0 mg. the right ovary enlarges by the hypertrophy of the medullary tissue and tends to assume a testis-like shape. The left ovary, on the contrary, remains normal in form and histology. The oviducts are usually typical and the Wolffian ducts are hypertrophied only slightly or not at all. Generally when the dosage exceeds 1.0 mg. both the right ovary and the medulla of the left ovary undergo hypertrophy and the cortex of the left shows changes of a degenerative nature. Both ovaries now assume a testis-like form, the right more so than the left (Fig. 4). The 23 embryos histologically examined may be classified into three grades of effects: (1) Those in which the ovarian cortex of the left gonad is generally thinner than normal, and sterile sex cords (presumably of cortical origin) are adjacent to the medulla. The oviducts are more or less rudimentary and the Wolffian ducts distended with fluid. (2) Embryos in which the ovarian cortex of the left gonad is somewhat degenerate and underlain with sterile sex cords. At the hilus of the gonad the medullary tissue has transformed into solid cords containing germ cells (potential testicular

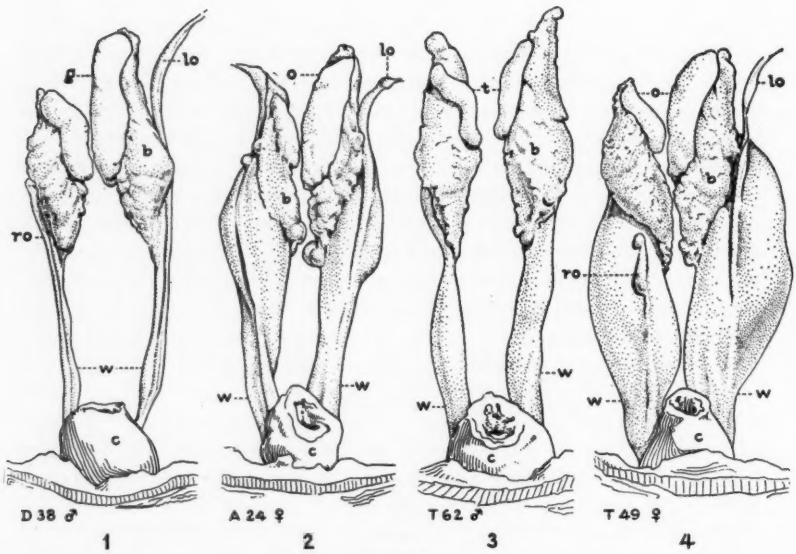

FIGURE 1

Urinogenital system of a 17-day genetic male embryo treated with 1.2 mgs. of dehydroandrosterone. Both right (ro) and left (lo) oviducts well developed; Wolffian ducts (w) moderately swollen; left gonad (g) ovary-like in form, histologically an ovotestis. b, left Wolffian body; c, cloaca. × 3.7.

FIGURE 2

Urinogenital system of a 17-day genetic female given 0.75 mg. of androsterone. Both right and left (o) ovaries have assumed a testis-like form; left oviduct (lo) greatly inhibited—posterior half missing; both Wolffian ducts (w) much distended with fluid. b, right Wolffian body; c, cloaca. × 3.7.

FIGURE 3

Urinogenital system of a 17-day genetic male treated with 1.0 mg. testosterone propionate. Testes (t) small but normal in form. Wolffian bodies (b) and ducts (w) swollen. c, cloaca. × 3.7.

FIGURE 4

Urinogenital system of a 17-day genetic female treated with 2.0 mgs. of testosterone propionate. Ovaries (o) decidedly testicular in form; oviducts, particularly the left (lo), have undergone extreme retrogression; ro, right oviduct; Wolffian bodies (b) and especially the ducts (w) greatly hypertrophied. c, cloaca. × 3.7.

cords). The left oviduct is quite rudimentary, the right either typical or longer than usual. The Wolffian ducts are usually much distended with fluid. (3) Embryos in which cortex of the left gonad is generally more degenerate (even absent over anterior portion) than in the preceding grade. Sterile cords (cortical) are usually present in the outer surface of the medulla and a region of distinct testicular cords with germ cells is seen at the hilus (Fig. 5). Testicular cords likewise appear in the hypertrophied medullary tissue of the right ovary. The left oviduct is generally reduced to a short rudimentary ostial portion containing a lumen, the remainder consisting of oviducal ligaments only; the right, on the contrary, is usually increased in length. The Wolffian ducts and many of the mesonephric tubules become enormously swollen. See figure 4. In general embryos exhibiting this grade of effect occur with a higher frequency when the dosage approaches 2.0 mgs. Finally it should be noted for the embryos of these grades, that the posterior end of the left ovary often exhibits a higher degree of modification in the male direction than the anterior end.

Genetic Males.—The Wolffian ducts and certain mesonephric tubules of the male embryos hypertrophy as they do in the genetic females. The gonads and oviducts, however, respond quite differently to the different hormones. With testosterone propionate the testes are reduced in size but show no essential change in form or structure (Fig. 3). The oviducts never persist. With androsterone and dehydroandrosterone, however, a strong feminizing action is seen which is very similar to that of oesterone and oestriol (Willier, *et al.*[2]). The left testis changes into a flattened ovary-like body consisting of ovarian and testicular tissues (ovotestis). The right testis remains histologically unchanged until the left testis is strongly feminized whereupon it becomes reduced in size, assumes an ovarian shape and develops some ovarian medullary tissue. The oviducts persist throughout their length and may even hypertrophy. The male thus comes to resemble closely a normal female (Fig. 1).

Degree and Order of Sex Transformation of the Females.—Although a histological study reveals considerable variation in the degree of intersexuality attained in the genetic female embryos for a given dosage, in general it is roughly proportional to the quantity of male hormone administered. The hormones, except testosterone propionate when larger doses are required, are nearly equally effective in producing a given grade of intersexuality. The minimum effective dose of androsterone and dehydroandrosterone is found to be about 0.19 mg. Although this was not ascertained for testosterone propionate a higher dose is indicated since doses between 0.25 and 0.40 mg. were found to be ineffective in nine embryos examined. Furthermore doses of 2.4 mgs. do not bring about any greater effect in the ovary at least than 1.0 mg. of androsterone and de-

hydroandrosterone. The male hormones bring about only a partial sex reversal of the genetic females even though administered in doses as high as 2.0 mgs. and more. This large quantity contrasts strikingly with the action of oestrone and oestriol which in doses of much less than 1.0 mg. may completely feminize a genetic male.

As a rule the first noticeable effect produced in the genetic females is a hypertrophy of the right ovary and of the Wolffian ducts. The left ovary and left oviduct are generally unaffected. Higher doses are necessary to bring about changes in the left ovary and left oviduct. In such cases the ovarian cortex and left oviduct are more or less inhibited and accompanied by structural changes in the ovarian medulla and a distention of both Wolffian ducts with fluid. In low grade modifications the medulla of the left ovary merely hypertrophies but in the higher grades where cortex is more strongly inhibited, the medullary tissue in the hilar region develops into testicular cords (Fig. 5); and many scattered testicular cords likewise develop in the medullary tissue of the right ovary. The formation of testicular cords in the medulla of the left ovary farthermost from the ovarian cortex may be indicative of a diminution in the extent of the inhibitory influence which the latter, from ovariotomy studies in the fowl, is known to have upon the ovarian medulla. On theoretical grounds it would be expected that as the ovarian cortex is inhibited more and more by the male hormones the transformation of medulla into testicular cords would spread from the hilus toward the surface. It is interesting to point out that when a testis is converted into an ovary by the action of oestrone or oestriol the order is reversed. That is, the transformation of testicular cords into ovarian medulla proceeds in the direction from the superimposed cortex inward toward the hilus, the cords there retaining their male form last.

Dual Physiological Action.—From the results it is seen that androsterone and dehydroandrosterone have both masculinizing and feminizing effects, whereas testosterone propionate has a masculinizing effect only upon the differentiating gonads and gonoducts. The possibility that testosterone propionate in the concentrations used may have a feminizing effect also upon embryos of other breeds must be recognized since Wolff and Wolff[3,4] have shown that acetate of testosterone is quantitatively less effective in producing both intersexual males and females of embryos of the Leghorn breed than in F_1 embryos of the cross Light Sussex females $\times$ Rhode Island Red males. Except for a more pronounced hypertrophy on the Wolffian ducts, androsterone is equally as effective as dehydroandrosterone in producing masculinizing and feminizing changes. Testosterone propionate is not greatly different from the other two male sex hormones, except for quantitative differences already noted, in producing masculinizing effects.

The difference in action of androsterone and dehydroandrosterone on the female components of genetic males and females is quite puzzling. As has been noted, these androgens bring about the development of ovarian

FIGURE 5

Ovotestis of a genetic female treated with 2.0 mgs. of testosterone propionate. Note mass of testicular cords in hilar portion of medulla, i.e., adjacent to adrenal (lowermost tissue in figure). Ovarian cortex thinner than normal. × 210.

cortex and the persistence of the oviducts in genetic males. In genetic females, on the contrary, they have an inhibitory action on these components. That is, the action of these substances in genetic females is wholly masculinizing in nature, whereas in genetic males both feminizing

and masculinizing effects are seen, the former being greater than the latter. The significance of these findings remains for future study.[5]

[1] Willier, B. H., Gallagher, T. F., and Koch, F. C., *Proc. Nat. Acad. Sci.*, **21**, 625–631 (1935).

[2] Willier, B. H., Gallagher, T. F., and Koch, F. C., *Physiol. Zoöl.*, **10**, 101–122.

[3] Wolff, E., and Wolff, Em., *C. R. Soc. Biol.*, **123**, 1191–1193.

[4] Wolff, E., and Wolff, Em., *Ibid.*, **124**, 367–369.

[5] The principal conclusions presented in this paper were communicated to the National Academy of Science in October, 1937 (*Science*, **86**, 409).

THE GENERALIZED CLEBSCH-GORDAN FORMULA

By F. D. Murnaghan

Department of Mathematics, The Johns Hopkins University

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The formula of Clebsch-Gordan which furnishes the analysis of the Kronecker product of any two irreducible representations of the two-dimensional unimodular linear group is one of the most important results of group theory in regard to the application of this theory to quantum mechanics; indeed Weyl, in his book on Group Theory and Quantum Mechanics (English edition pp. 128–129) affirms that "it may justly be considered as the fundamental mathematical formula for the classification of atomic spectra and for the theory of the valence bond." We point out here that it is but a special case of a general formula giving the analysis of the Kronecker product of any two irreducible rational, integral representations of the full n-dimensional linear group *which depend on a single label;* the typical rational integral representation $\Gamma_{(\lambda)}$ of the full n-dimensional linear group depends on j labels $(\lambda_1, \ldots, \lambda_j)$, $j = 1, 2, \ldots n$ and the generalized Clebsch-Gordan formula has reference to those particular representations for which $j = 1$.

There is also a Clebsch-Gordan formula which furnishes the analysis of the Kronecker product of any two irreducible representations of the 3-dimensional rotation group. We point out here that this is but a special instance of a general formula which furnishes the analysis of the Kronecker product of any two irreducible representations of the full n-dimensional real orthogonal group *which depend on a single label;* the typical irreducible representation $\Gamma_{(\lambda)}$ of the full n-dimensional real orthogonal group depends on j labels $(\lambda_1, \ldots \lambda_j)$, $j = 1, \ldots k$, where $k = \frac{n}{2}$ or $\frac{n-1}{2}$ according as n is even or odd and the generalized Clebsch-Gordan formula has reference to those representations for which $j = 1$. The n-dimensional rotation

group is an invariant subgroup, of dimension 2, of the full real, n-dimensional, orthogonal group so that our generalization is in two directions

(a) from $n = 3$ to n general,

(b) from the rotation group (= proper orthogonal group) to the full real orthogonal group.

The generalization (a), in particular, is not trivial since the whole theory of representations of the orthogonal group is dominated by the number k which for $n = 2$ or 3 is 1 but which > 1 if $n > 3$. We merely state results here; the appropriate demonstrations will be given in a paper to appear shortly in the *American Journal of Mathematics*.

The theorem for the full linear group is well known and is as follows: denoting by $D(\lambda)$ the representation which is specified by the numbers (λ) we have

$$D(\lambda_1) \times D(\lambda_2) = D(\lambda_1, \lambda_2) + D(\lambda_1 + 1, \lambda_2 - 1) + \ldots + D(\lambda_1 + \lambda_2).$$

For the two dimensional unimodular group $D(\mu_1, \mu_2) = D(\mu_1 - \mu_2)$, simply because the characteristic numbers of any matrix of this group are each the reciprocal of the other, so that

$$D(\lambda_1) \times D(\lambda_2) = D(\lambda_1 - \lambda_2) + D(\lambda_1 - \lambda_2 + 2) + \ldots + D(\lambda_1 + \lambda_2)$$

which is the Clebsch-Gordan formula.

Turning to the full real n-dimensional orthogonal group the generalized Clebsch-Gordan formula is

$$\begin{aligned} D(\lambda_1) \times D(\lambda_2) = {} & D(\lambda_1 - \lambda_2) + D(\lambda_1 - \lambda_2 + 2) + \ldots \quad + D(\lambda_1 + \lambda_2) \\ & + D(\lambda_1 - \lambda_2 + 1,1) + D(\lambda_1 - \lambda_2 + 3,1) + D(\lambda_1 + \lambda_2 - 1,1) \\ & + D(\lambda_1 - \lambda_2 + 2,2) + \ldots \\ & \cdots\cdots\cdots \\ & + D(\lambda_1,\lambda_2). \end{aligned}$$

E.g., $D(3) \times D(2) = D(5) + D(3) + D(1) + D(4,1) + D(2,1) + D(3,2)$.

When $k = 1$ (i.e., when $n = 2$ or 3) the $D(\mu_1, \mu_2)$ depending on two labels must be modified as follows: when $n = 2$, all $D(\mu_1, \mu_2)$ for which $\mu_2 > 2$ are dropped; all $D(\mu_1, 2)$ are replaced by $-D(\mu_1)$; all $D(\mu_1, 1)$ for which $\mu_1 > 1$ are dropped; and finally $D(1, 1)$ is replaced by $\epsilon D(0)$ where $\epsilon = \pm 1$ according as the element of our group belongs to the rotation subgroup or not. Hence when $n = 2$

$$\begin{aligned} D(\lambda_1) \times D(\lambda_2) &= D(\lambda_1 - \lambda_2) + D(\lambda_1 + \lambda_2); \ \lambda_1 \neq \lambda_2 \\ D(\lambda_1) \times D(\lambda_1) &= D(0) + D^*(0) + D(2\lambda_1) \end{aligned}$$

the star denoting the associated representation (so that $D^*(0)$ is the alternating one-dimentional representation, $D(0)$ being the identity representation). When $n = 3$, on the other hand, all the $D(\mu_1, \mu_2)$ for which $\mu_2 > 1$ are dropped and all the $D(\mu_1, 1)$ are replaced by $D^*(\mu_1)$ so that

$$D(\lambda_1 - \lambda_2) + D(\lambda_1 - \lambda_2 + 2) + \ldots + D(\lambda_1 + \lambda_2)$$

$$D(\lambda_1) \times D(\lambda_2) =$$

$$+ D^*(\lambda_1 - \lambda_2 + 1) + D^*(\lambda_1 - \lambda_2 + 3) + \ldots + D^*(\lambda_1 + \lambda_2 - 1)$$

which is the Clebsch-Gordan formula for the 3-dimensional full real orthogonal. For the rotation subgroup the stars may be removed (since two associated representations of the full group coincide over the rotation subgroup) and we recover the ordinary Clebsch-Gordan formula.

THE ANALYSIS OF REPRESENTATIONS OF THE REAL ORTHOGONAL GROUP

By F. D. Murnaghan

Department of Mathematics, The Johns Hopkins University

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Each irreducible rational integral representation $D(\lambda)$ of the full linear n-dimensional group furnishes, by the principle of selection, a representation, in general reducible, of the full real n-dimensional orthogonal subgroup. We indicate here the analysis of this representation of the orthogonal group. On denoting by k the number $\frac{n}{2}$ if n is even and the number $\frac{n-1}{2}$ if n is odd, the analysis of $D(\lambda_1, \ldots, \lambda_j)$, $j = 1, 2, \ldots k$, is obtained as follows: let ξ_p, $p = 1, 2, \ldots j$, be an operator which diminishes by unity the label λ_p and let $\Delta(\mu)$ denote the irreducible representation of the full real orthogonal n-dimensional group which is specified by $(\mu) = (\mu_1, \mu_2, \ldots)$. Then

$$D(\lambda_1, \ldots, \lambda_j) = \left\{ \prod_{p \leq q}^{j} (1 - \xi_p \xi_q)^{-1} \right\} \Delta(\lambda_1, \ldots, \lambda_j).$$

As examples we cite the following. The case $j = 1$ is trivial

$$D(\lambda_1) = (1 - \xi_1^2)^{-1} \Delta(\lambda_1) = \Delta(\lambda_1) + \Delta(\lambda_1 - 2) + \Delta(\lambda_1 - 4) + \ldots$$

When $j = 2$ it is convenient to first operate with $(1 - \xi_2^2)^{-1}$ then with $(1 - \xi_1\xi_2)^{-1}$ and finally with $(1 - \xi_1^2)^{-1}$. In this way we find, for example,

$$D(4, 2) = \Delta(4, 2) + \Delta(4) + \Delta(3, 1) + \Delta(2^2) + 2\Delta(2) + \Delta(0).$$

When $k = 1$ ($n = 2$ or 3) so that $j(= 2) > k\ (= 1)$ the $\Delta(\mu_1, \mu_2)$ must be modified as follows: when $n = 2$ all $\Delta(\mu_1, \mu_2)$ for which $\mu_2 > 2$ are dropped;

all $\Delta(\mu_1, 2)$ are replaced by $-\Delta(\mu_1)$; all $\Delta(\mu_1, 1)$ for which $\mu_1 > 1$ are dropped; and $\Delta(1, 1)$ must be replaced by $\Delta^*(0)$, the star indicating the associated representation; e.g., when $n = 2$

$$D(4, 2) = \Delta(2) + \Delta(0)$$

(the check by dimensions being $3 = 2 + 1$). If $n = 3$ all $\Delta(\mu_1, \mu_2)$ for which $\mu_2 > 1$ are dropped, and all $\Delta(\mu_1, 1)$ are replaced by $\Delta^*(\mu_1)$. E.g., when $n = 3$,

$$D(4, 2) = \Delta(4) + \Delta^*(3) + 2\Delta(2) + \Delta(0)$$

(the check by dimensions being $27 = 9 + 7 + 10 + 1$).

The modifications just mentioned are only necessary when $j > k$; for a general value of n the necessary modifications are of the same character. When $n = 2k$ is even, every $\Delta(\mu_1, \ldots \mu_k, \mu_{k+1})$ for which $\mu_{k+1} > 2$ is dropped; every $\Delta(\mu_1, \ldots, \mu_k, 2)$ is replaced by $-\Delta(\mu_1, \ldots \mu_k)$; every $\Delta(\mu_1, \ldots, \mu_k, 1)$ for which $\mu_k > 1$ is dropped and every $\Delta(\mu_1, \ldots \mu_{k-1}, 1^2)$ is replaced by $\Delta^*(\mu_1, \ldots \mu_{k-1})$. When $n = 2k + 1$ is odd, every $\Delta(\mu_1, \ldots, \mu_k, \mu_{k+1})$ for which $\mu_{k+1} > 1$ is dropped while each $\Delta(\mu_1, \ldots, \mu_k, 1)$ is replaced by $\Delta^*(\mu_1, \ldots \mu_k)$. Similar, but of necessity more elaborate, "modification rules" may be given when $j > k + 1$ (the maximum value of j being n).

We close with the following remarks: The analysis of the representations of the full real orthogonal group which are obtained by the principle of selection from the irreducible rational integral representations of the full linear group furnishes the analysis of the representations of the rotation (= proper real orthogonal) group which are similarly obtained. The method here described is also available (and simpler in application) for the complex group.

NATURAL SYSTEMS

BY ALFRED L. FOSTER

DEPARTMENT OF MATHEMATICS, UNIVERSITY OF CALIFORNIA

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1. A system with single composition $(N, \circ)$, is a *natural system* if it can be faithfully realized by some non-empty set of natural numbers $\geqslant 2$ which is closed with respect to (and where $\circ$ is realized as) ordinary multiplication. In connection with natural systems, the definitions of such terms as are borrowed from the ordinary natural number system will be clear by analogy, and need not be explicitly given in this summary. There

are then exactly $\aleph_0$ (abstractly) different natural systems $N_1, N_2, \ldots, N_{\aleph_0}$, where N_k is that system having exactly k prime elements.

A *regular ordering* of N is an infinite sequence consisting of the elements of N, each exactly once, and such that $\xi < \eta$ implies $\rho\xi < \rho\eta$, for all elements ξ, η, ρ of N, where $<$ is an abbreviation for *precedes*, and $\rho\xi$ for $\rho \circ \xi$.

THEOREM 1. *In a regular ordering of* (N, ∘) *each element is preceded by each of its proper divisors; in particular the first element must be a prime.*

Two regular orderings of $(N, \circ)$ are *essentially different* if they cannot be made identical by any relettering (permutation) of their primes.

As an important step in the study of the structure of the regular orderings of $(N, \circ)$, a problem which bears heavily on both the theory of integers and of real numbers, this summary deals with principal concepts and results on the simplest non-trivial case, the natural system N_2. The main theorems are 4, 6, 9.

2. Let α, β denote the prime elements of and E the class of all essentially different regular orderings of M_2, i.e., the class of all orderings of N_2 for which $\alpha < \beta$. An *inequality* is a relation either of the form $\alpha^m < \beta^{m'}$, or else $\beta^{n'} < \alpha^n$. (Here $\alpha^m = \alpha \cdot \alpha \cdot \ldots \alpha$, m factors; $m = 1, 2, \ldots$). Each element of E is uniquely determined by a suitable (necessarily infinite) list of inequalities. Again, certain subclasses of E are definable by a finite list of inequalities. Such subsets of E we call *rational*. Lists of inequalities which define the same subset of E are *equivalent*.

A *reduced* list is one consisting either of a single inequality of type (1°): $(\alpha^m < \beta^{m'})$, or else of a pair of inequalities of type (2°): $\begin{pmatrix} \alpha^m < \beta^{m'} \\ \beta^{n'} < \alpha^n \end{pmatrix}$, where in each case we demand $(m, m') = 1$ (i.e., relatively prime), $m' \leqslant m$, $(n, n') = 1$, $mn' < m'n$.

THEOREM 2. *Each rational subclass of* E *may be defined by exactly one reduced list. Conversely, each reduced list defines exactly one rational subclass of* E.

A *primitive* list is one consisting either of a single inequality of form (*i*): $(\alpha^m < \beta)$, or else of a pair of inequalities of form (*ii*): $\begin{pmatrix} \alpha^m < \beta^{m'} \\ \beta^{n'} < \alpha^n \end{pmatrix}$, with $m' \leqslant m$, and $mn' + 1 = m'n$. A primitive list is obviously reduced. A (*rational*) *primitive subclass* (of type (*i*) or (*ii*), respectively) of E is one whose reduced defining list is primitive (of type (*i*) or (*ii*), respectively). With the exception of the last theorem, 9, primitive class is used to mean rational primitive class. In theorem 9, however, for symmetry of expression, we call a single element of E an *irrational* primitive class.

3. The pair $[\alpha^r, \beta^{r'}]$ is the *first undetermined pair* of a rational subclass R of E if r is the smallest integer for which an x exists such that $\alpha^r < B^x$ for at least one, and also $\beta^x < \alpha^r$ for at least one element of R, and r' is the smallest x satisfying the above. The integers r, r' of $[\alpha^r, \beta^{r'}]$

clearly satisfy: $(r, r') = 1$, and $r > r'$. The rational number $r/r' > 1$ we call the *characteristic number* of the rational subclass R.

THEOREM 3. *The characteristic number of a primitive class* P *is the rational integer* $m + 1$ *if* P *is of type* (i), *and the rational non-integer* $\frac{m+n}{m'+n'}$ *if* P *is of type* (ii).

By use of this theorem one proves the basic

THEOREM 4. *Each rational number* > 1 *is the characteristic number of one and only one primitive subclass of* E. *Moreover, to a rational integer (respectively non-integer) corresponds a primitive subset of type* (i) (*respectively* (ii)).

Accordingly we uniquely denote by $E_\mathfrak{v}$ that primitive subclass of E whose characteristic number is the rational number $\mathfrak{v} > 1$, and in this way exhaust the primitive subclasses.

4. As examples of numerous decomposition theorems we mention two.

THEOREM 5. *If the logical product of two primitive subclasses of* E *is not empty, then one of the primitive subclasses is a subclass of the other.*

THEOREM 6. *Every rational subclass of* E *can be expressed as the logical sum of a finite number of disjoint primitive classes the logical sum of no two of which is again a primitive subclass. Moreover, this decomposition is unique.*

5. Any single element J of E may be defined by a denumerably infinite list of pairs of inequalities, such that each pair defines a primitive class $E_{\mathfrak{v}_i}$, and such that in the sequence $E_{\mathfrak{v}_1}, E_{\mathfrak{v}_2}, \ldots$ each $E_{\mathfrak{v}_{n+1}}$ is a proper subset of $E_{\mathfrak{v}_n}$ where $\mathfrak{v}_n$ is the characteristic number of the principal class $E_{\mathfrak{v}_n}$. Such a sequence of primitive subclasses we call *regular*. By use of decomposition theorems one shows

THEOREM 7. $\lim_{n \to \infty} \mathfrak{v}_n$ *exists, and is independent of the regular sequence of principal classes which is used to define the element* J *of* E.

We then call $\lim_{n \to \infty} \mathfrak{v}_n$ the *characteristic number of the element* J *of* E. From theorem 4 we then get

THEOREM 8. *The characteristic number of a single element of* E *is an irrational number.*

Then by another appeal to decomposition theorems one extends theorem 4 to

THEOREM 9. FUNDAMENTAL THEOREM. *To each primitive subclass* of* E *corresponds a unique real number* > 1, *the characteristic number of the subclass. Conversely, each real number* > 1 *is the characteristic number of a unique primitive subset of* E. *Moreover, to an irrational number corresponds an irrational primitive subclass, while to a rational integer (non-integer) corresponds a rational primitive subset of type* (i) (*type* (ii)).

* See closing remarks of §2.

EXTENSIONS OF MEASURE

By H. M. MacNeille

Department of Mathematics, Harvard University

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Introduction.—One of the elementary applications of measure theory is, using two dimensional terminology, the determination of areas in the Euclidean plane. Initially, area is defined only for certain rectangular or elementary figures. It is the object of the theory of measure to extend the definition of area to as large a class of subsets of the plane as possible. The set of figures which can be formed by a finite number of rectangles with sides parallel to fixed directions and with vertices with rational coördinates is dense and denumerable This set plays a rôle in the theory of measure analogous to that of the rational numbers in the construction of the real numbers. It is the object of this note to give an abstract formulation for measure theoretical constructions analogous to the various methods of defining real numbers in terms of rationals.[1]

One starts with an abstract system of point sets which has the pertinent properties of the set of rectangular figures in the plane. This set is extended by methods analogous to those by which the real numbers are obtained. The elements of the extended sets so obtained are abstract, that is, they are not point sets, as were the elements of the original set. The next step is the assignment of point sets to these abstract elements. Certain of these point sets may be ordinate sets. To these, functions can be assigned and, by this means, integration[2] is introduced. The integral of a non-negative function is the measure, or area, of its ordinate set. In particular, the ordinate set of a step function is a rectangular figure.

A real number may be defined as a sequence of nested intervals of rationals. The analogue of this method yields the theory of content and Riemann integration. The analogue of the definition of real numbers by fundamental, or Cauchy, sequences gives Lebesgue measure and integration. The method of cuts does not lend itself readily to interpretation in terms of measure. The method of bounded monotone sequences, when applied first with ascending and then with descending sequences, is, in essence, the classical method for the definition of Lebesgue measure. A precise formulation of the first two of these methods follows.

Definitions and Notation.—The domain of discussion is a basic set, I, of points. Subsets of I are denoted by a, b, c, ... The symmetric difference, $a - b$, is the set of points in either a or b but not in both. $a + b$ is the set of points in either a or b or in both. The iteration of this operation either a finite or an infinite number of times is denoted by Σ. ab is the set of points in both a and b and iteration of this operation is denoted

by II. If every point of a is a point of b, then $a \subset b$. If a and b contain the same points, then $a = b$. The identity $a + b = a - b - ab$ and the equivalence of $a \subset b$ and $a = ab$ may be used to define the operation $+$ and the relation $\subset$.

A Boolean ring[3] is an algebraic ring in which $aa = a$ for every element in the ring. Multiplication in such a ring is necessarily commutative and addition is modulo 2. Consequently, addition and subtraction are the same and the minus sign can be used throughout to denote this operation. By this convention ring addition can be associated with point set symmetric difference and the plus sign reserved for point set addition. A system of point sets is a Boolean ring if point set symmetric difference is identified with ring addition, point set multiplication, with ring multiplication and point set equality, with ring equality, provided that the system is closed under these operations. In general, not all the subsets of the basic set will be elements of a given Boolean ring of point sets. In fact, the void subset, 0, is the only subset which is necessarily an element of such a ring. The letter K will be used to denote a Boolean ring of subsets of I for the elements of which a real valued function, the absolute value, satisfying the following conditions is defined.

1. $|a| > 0$, if $a \neq 0$.
2. If $a = b$, then $|a| = |b|$.
3. $|a| = |a - ab| + |ab|$.

As consequences of these conditions, it follows that:

(a) If $a \subset b$, then $|a| \leq |b|$;
(b) $|a + b| = |a| + |b| - |ab| \leq |a| + |b|$;
(c) $|a - b| = |a| + |b| - 2|ab| \leq |a| + |b|$.

The absolute value in K is said to be completely additive if, in addition to Conditions 1, 2 and 3, the following condition holds.

4. If $a = \sum_{i=1}^{\infty} a_i$ and $a_i a_j = 0$ for $i \neq j$, then $|a| = \sum_{i=1}^{\infty} |a_i|$.

Conditions equivalent to 4 follow:

4′. If $a = \sum_{i=1}^{\infty} a_i$, then $|a| = \lim_{n \to \infty} |\sum_{i=1}^{n} a_i|$;

4″. If $[a_i]$ is a sequence such that $a_i \subset a_j$ for $i \geq j$ and $\lim_{i \to \infty} |a_i| = k > 0$, then there is a point common to every a_i.

Condition 4 is a covering property similar to the Heine-Borel theorem for open sets. Condition 4″ is analogous to the Cantor property of descending sequences of closed sets. In fact, measurable sets may be re-

garded as both open and closed in a suitably defined discrete space. Nothing in Conditions 4, 4′ and 4″ implies the existence of infinite sums or products in K.

Any system of elements for every pair of which a real valued function, $\rho(a, b)$, is defined such that $\rho(a, a) = 0$, $\rho(c, a) \leq \rho(a, b) + \rho(b, c)$ and in which equality is defined by the relation $a = b$ if $\rho(a, b) = 0$ is a metric space. If, by definition, $\rho(a, b) = |a - b|$, then K is a metric space.

Examples.—For an example of a system K, let I be n dimensional Euclidean space, E_n, of points (x_i), $i = 1, 2, \ldots, n$, where the x_i are real numbers. A half open interval in E_n is determined by two points (a_i) and (b_i) such that $a_i < b_i$ for all i, and consists of all points (x_i) such that $a_i \leq x_i < b_i$ for all i. The absolute value of an interval is defined as $\prod_{i=1}^{n} (b_i - a_i)$. If, for all i, a_i and b_i are rational, then the interval is said to be rational. Let $K(E_n)$ be the system whose elements are the sets in E_n which can be represented as the sum of a finite number of disjoint rational half open intervals. The absolute value of an element in $K(E_n)$ is the sum of the absolute values of the intervals by which it is represented. This definition leads to no ambiguities. $K(E_n)$ satisfies all the conditions for K and the absolute value is completely additive.

Let K and K' be Boolean rings of subsets of I and I' for which absolute values have been defined. Let $I'' = I \times I'$, the set of pairs of points, the first, from I, the second, from I'. If $a \epsilon K$ and $a' \epsilon K'$, let (a, a') represent the points in I'' formed by a point from a and a point from a'. Let $|(a, a')| = |a||a'|$. Denote the set of all such elements by $K \times K'$. Let a subset of I'' be an element of K'' if, and only if, it can be represented as the sum of a finite number of disjoint elements in $K \times K'$. The absolute value of an element in K'' is defined as the sum of the absolute values of the elements of $K \times K'$ by which it is represented. This definition[4] leads to no ambiguities. K'' fulfils all the conditions imposed on K and K'. In particular, if the absolute values in K and K' are completely additive, then so is the absolute value in K''. If K and K' are taken as $K(E_n)$ and $K(E_m)$, respectively, then K'' is $K(E_{n+m})$.

Extension by Sequences of Nested Intervals.—The extension of a system, K, by means of sequences of nested intervals, is now considered. The extended set will be denoted by L.

DEFINITION. $[a_n, b_n]$, $n = 1, 2, \ldots$, is a *sequence of nested intervals* in K if $a_n \subset a_m \subset b_m \subset b_n$, for $n \leq m$.

DEFINITION. The extended system, L, is defined as follows:

(*a*) The elements of L are the sequences of nested intervals in K for which $\lim_{n \to \infty} |a_n - b_n| = 0$;

(*b*) $[a_n, b_n] = [c_n, d_n]$, if $a_n \subset d_n$ and $c_n \subset b_n$;

(c) $[a_n, b_n] - [c_n, d_n] = [(a_n - c_n)(b_n - d_n), (b_n + d_n) - a_n c_n]$;
(d) $[a_n, b_n][c_n, d_n] = [a_n c_n, b_n d_n]$;
(e) $|[a_n, b_n]| = \lim_{n\to\infty} |a_n|$.

THEOREM. L *is a Boolean ring with absolute value. The correspondence* $a \longleftrightarrow [a_n, a_n]$, *where* $a_n = a$ *for every* n, *is a one to one mapping of* K *onto a subset of* L. *The algebraic operations, absolute value and equality are preserved by this mapping.* L *is closed to further extension by this method.*

The elements of L are not point sets. The next step is the assignment of subsets of I to the elements of L. The point set operations of the assigned sets must correspond to the algebraic operations in L of the elements to which the sets belong. The absolute value of an element in L will be the content of the point sets which belong to it.

DEFINITION. A subset, c, of I *belongs to* an element $[a_n, b_n]$ of L if $\sum_{n=1}^{\infty} a_n \subset c \subset \prod_{n=1}^{\infty} b_n$. If c belongs to $[a_n, b_n]$, then $|[a_n, b_n]|$ is the *content* of c.

Every element of L has at least one point set, $\sum_{n=1}^{\infty} a_n$, belonging to it. In general, not every subset of I will belong to an element of L. Let G be the class of subsets of I which belong to some element of L. Let Y be the class of point sets with content zero.

THEOREM. G *is a Boolean ring of point sets.* Y *is an ideal in* G. *The quotient ring* G/Y *is isomorphic with* L. K *is a subring of* G *and the absolute value of an element in* K *is equal to its content.*

When the given Boolean ring is $K(E_n)$, G is the class of sets in E_n for which Jordan content is defined. An effective extension is secured in this case. The Riemann integral of a function is the content of its ordinate set. The theory of Riemann integration can be developed from this point, the general procedure being to establish properties in $K(E_n)$, that is, for step functions, and then showing that the properties are preserved under the extension.

For the extension from K to G it is not necessary that the absolute value in K be completely additive. However, the complete additivity of the absolute value in K leads to the following theorem.

THEOREM. If the absolute value in K is completely additive, then so is it in G. Furthermore, if $[a_n, b_n]$ is any sequence of nested intervals and $\sum_{n=1}^{\infty} a_n = \prod_{n=1}^{\infty} b_n$, then $\lim_{n\to\infty} |a_n - b_n| = 0$.

Extension by Fundamental Sequences.—The extension, by fundamental sequences, of a system K with completely additive absolute value is considered next.

DEFINITION. A sequence, $[a_n]$, in K is a *fundamental sequence* if, for

every $\epsilon > 0$, an integer, $N(\epsilon)$, exists such that whenever $m > n > N(\epsilon)$ $|a_n - a_m| < \epsilon$.

DEFINITION. A sequence, $[a_n]$, in K is *absolutely convergent* if $\sum_{n=1}^{\infty} |a_n - a_{n+1}|$ is convergent.

THEOREM. In K, every absolutely convergent sequence is a fundamental sequence and every fundamental sequence contains an absolutely convergent subsequence.

No generality is lost by restricting the argument to absolutely convergent sequences instead of admitting the entire class of fundamental sequences.

DEFINITION. The extended set, M, is defined as follows:

(*a*) The elements of M are the absolutely convergent sequences in K;

(*b*) $[a_n] = [b_n]$, if $\lim_{n\to\infty} |a_n - b_n| = 0$;

(*c*) $[a_n] - [b_n] = [a_n - b_n]$;

(*d*) $[a_n][b_n] = [a_n b_n]$;

(*e*) $|[a_n]| = \lim_{n\to\infty} |a_n|$.

If K is regarded as a metric space, then M is the completion of K by the Cantor-Meray[5] process. However, in addition to this, the algebraic operations of K have also been extended to M. The extension from K to M, here defined by sequences, can equally well be formulated in terms of infinite series, that is, infinite symmetric differences.

THEOREM. M *is a Boolean ring with absolute value. Every fundamental sequence in* M *has a limit in* M. *The correspondence,* $a \longleftrightarrow [a_n]$, *where* $a_n = a$ *for all* n, *is a one to one map of* K *onto a subset of* M *which preserves the algebraic operations, absolute value and equality.* M *is closed to further extension by this method.*

The complete additivity of the absolute value in K is not necessary for the construction of M, but it is necessary if the measure of the point sets assigned to elements of M is to be uniquely defined.

DEFINITION. A subset, a, of I *belongs to* an element, $[a_n]$, in M if $\prod_{n=1}^{\infty} \sum_{i=n}^{\infty} a_i \supset a \supset \sum_{n=1}^{\infty} \prod_{i=n}^{\infty} a_i$. If a belongs to $[a_n]$, then $|[a_n]|$ is the *measure* of a.

Under this definition, if a belongs to $[a_n]$, then a contains every point which occurs in all but a finite number of terms of $[a_n]$ and all points which occur in but a finite number of terms, or not at all, are excluded from a. The remaining points may or may not be in a. Their measure is zero. At least one subset of I belongs to each element of L, namely $\sum_{n=1}^{\infty} \prod_{i=n}^{\infty} a_i$. In general, not every subset of I belongs to an element of M. Let H be the

class of subsets of I which belong to elements of M. Let Z be the class of sets of measure zero.

THEOREM. *If the absolute value in* K *is completely additive, then so is the measure in* H. *If the void set belongs to* $[a_n]$, *then* $|[a_n]| = 0$.

THEOREM. If a belongs to $[a_n]$ and b belongs to $[b_n]$, then ab belongs to $[a_nb_n + (a_n - a_na_{n+i})] = [a_nb_n]$ and $a - b$ belongs to

$$[a_n - b_n - b_n(a_n - a_{n+i})(b_n - b_{n+i})] = [a_n - b_n].$$

THEOREM. H *is a Boolean ring of point sets.* Z *is an ideal in* H. *The quotient ring* H/Z *is isomorphic with* M. K *and* G *are subrings of* H *and, in* G, *the content of a set is equal to its measure.*

When the given system is $K(E_n)$, H is the class of subsets of E_n for which Lebesgue measure is defined and finite, and the measure in H is Lebesgue measure. The theory of Lebesgue integration can be developed from this point by assigning functions to Lebesgue measurable ordinate sets.

[1] The possibility of such constructions has been remarked by Gillis, J., *Quart. Jour. Math.*, **7**, 192, §2 (1936) and Glivenko, V., *Am. Jour. Math.*, **58**, 802, §7 (1936).

[2] In this paper, integration has been made subordinate to measure. Analogous constructions in which integration is fundamental are possible. Measure is introduced by means of characteristic functions. Such a construction, by means of monotone sequences, is given by Daniel, P. J., *Ann. Math.*, **19**, 279–294 (1917–18) and **21**, 203–220 (1919–20). The method of fundamental sequences has been used to define an integral by Dunford, N., *Trans. Am. Math. Soc.*, **37**, 441–453 and **38**, 600–601 (1935).

Constructions of this type by M. H. Stone and N. Wiener have not been published.

[3] For formal algebraic properties of Boolean rings, see Stone, M. H., *Trans. Am. Math. Soc.*, **40**, 37–111, Chapter I (1936).

[4] For the definition of measure in product spaces, see Lomnicki, Z., and Ulam, S., *Fund. Math.*, **23**, 237–278 (1934).

[5] Hausdorff, F., *Mengenlehre*, Leipzig, Gruyter, (2nd. Ed., 1927), p. 106.

REPRESENTATION AND EQUIVALENCE OF FORMS

BY RUFUS OLDENBURGER

INSTITUTE FOR ADVANCED STUDY

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This paper is concerned with the expressibility of a form F with coefficients in a given field as a sum S of powers of linear forms, and the determination of various possible representations S of F. These representations are employed to give necessary and sufficient conditions for the equivalence of forms of any degree under non-singular linear transformations in a given field. Until the present paper no such conditions were obtained for the classical problem of equivalence of general forms of degree higher than 2. It was for the purpose of solving this general equivalence problem that the

author developed the theory of higher dimensional matrices in earlier papers.

1. *Existence of Representations.*—The matrix $A = (a_{ij \ldots m})$ associated with a form $F = a_{ij \ldots m} x_i x_j \ldots x_m [i, j, \ldots m = 1, 2, \ldots, n]$ is said to be *symmetric* if the value of an element of A is invariant under permutation of its subscripts. Let S denote the sum

$$S = \lambda_1 L_1^p + \ldots + \lambda_\sigma L_\sigma^p, \tag{1.1}$$

where $\lambda_1, \ldots, \lambda_\sigma$ are coefficients, and $L_1, \ldots, L_\sigma$ are linear forms. We shall say that a form F can be written in a field ϕ as a *sum of* p*th powers of linear forms* if there exists an S such that $F = S$, where $\lambda_1, \ldots, \lambda_\sigma$ and the coefficients of $L_1, \ldots, L_\sigma$ are in ϕ. Our basic theorem on the existence of representations of F is the following.

THEOREM 1.1. *Let* [F] *denote the class of forms of degree* p *with symmetric matrices whose coefficients are in a field* ϕ. *Let* [F_S] *denote the sub-class of forms of* [F] *which can be written in* ϕ *as sums of* p*th powers of linear forms. If* ϕ *is composed of* p *or more elements the classes* [F] *and* [F_S] *are identical.*

Writing $L_i = a_{ij} x_j$ and F as above, the equation $F = S$ is satisfied if the system of equations

$$\sum_{\alpha=1}^{\sigma} \lambda_\alpha a_{\alpha i} a_{\alpha j} \ldots a_{\alpha m} = a_{ij \ldots m}, \tag{1.2}$$

which are linear in the λ's is satisfied. There are as many equations in (1.2) as distinct elements N in the general symmetric matrix. Let $\sigma = N$. By restricting the elements of $(a_{\alpha i})$ in a very special way we can write the matrix M of coefficients of the λ's in (1.2) as a matrix M' with diagonal minors of the form

$$K = (\alpha_i^r \alpha_j^s \ldots \alpha_m^t),$$

where $(r, s, \ldots, t)$ and $(i, j, \ldots, m)$ form multipartite row and column indices of K, respectively, and $i, \ldots, m, r, \ldots, t$ are indices ranging over sets of values subject to the restrictions

$$\begin{aligned} i + j + \ldots + m &\leqq p - 1, \\ i, j, \ldots, m &\geqq 0, \\ r + s + \ldots + t &\leqq p - 1, \\ r, s, \ldots, t &\geqq 0. \end{aligned}$$

The non-diagonal minors of M' are zero. By an induction process in which K is reduced under elementary transformations to a matrix whose diagonal minors are of the same type as K we prove that the determinant $|M|$ is non-singular if $\alpha_0 = 1$, and $\alpha_0, \ldots, \alpha_{p-1}$ are distinct.

That the classes $[F]$ and $[F_S]$ are not always identical follows from the fact that x^2y cannot be written as a sum S for the field composed of the

elements 0, 1 with characteristic 2. Let $[F]_{np}$ denote the class of forms of degree p in n variables with coefficients in ϕ. Let $[F_S]_{np}$ denote the subclass of $[F]_{np}$ of forms F which have a representation (1.1) in ϕ. That there exist values of n and p such that $[F]_{np}$ and $[F_S]_{np}$ are identical for every field ϕ follows from the fact that these classes are equal for binary forms of the fourth degree and any field.

2. *Properties of Representations.*—If in a field ϕ we can write a form F as (1.1) we shall say that F has a *representation* $[\lambda_\alpha, A]$ in ϕ where λ_α denotes the set $\lambda_1, \ldots, \lambda_\sigma$, and A is the matrix $(a_{\alpha i})$ of coefficients of the $L_\alpha = a_{\alpha i}x_i$ in (1.1). A representation $[\lambda_\alpha, A]$ of F for which σ takes on its smallest value is said to be a *minimal representation* of F in ϕ. Let a field for which the symmetric matrix of a form F of degree p in n variables is unique be termed an (n, p)-*proper field*. From the rank of the matrix M of coefficients of the λ's in equations (1.2), and the non-vanishing of the λ's we prove the theorem which follows.

THEOREM 2.1. *Let a form* F *be of degree* p *in* n *variables. In a minimal representation* $[\lambda_\alpha, A]$ *of* F *for an* (n, p)*-proper field the* λ*'s are uniquely determined by* A.

We shall understand that "equivalence" of forms means equivalence under non-singular linear transformations on the variables occurring in the forms. Since m by n matrices A and A' where $m \geqq n$ are related by an equation $A' = UA$, where U is non-singular, and further a minimal representation $[\lambda_\alpha, A]$ transforms into a minimal representation $[\lambda\alpha, A']$ under non-singular linear transformations we derive the following equivalence theorem.

THEOREM 2.2. *Let* $[\lambda_\alpha, A]$ *be a minimal representation of a form* F *in* ϕ. *For the equivalence of a form* F′ *to* F *in* ϕ *it is necessary that* F′ *have a representation* $[\lambda_\alpha, A']$ *for some* A′ *with respect to* ϕ. *If this necessary condition is satisfied the forms* F *and* F′ *are equivalent in* ϕ *if and only there exist non-singular matrices* U, X *with elements in* ϕ *such that*

$$A' = UAX,$$

where $[\lambda_\alpha, UA]$ *is a representation of* F.

3. *Non-Singular Representations.*—If $[\lambda_\alpha, A]$ is a minimal representation of F in a field ϕ, then $[\lambda_\alpha', DJA]$ is a minimal representation of F in ϕ, where the λ_α' are equal in some order to the λ_α multiplied by pth powers of non-zero elements in ϕ, J is a permutation matrix, and D is a diagonal matrix depending on the λ_α'. If A is non-singular the only other minimal representations of a form F of degree p in n variables for an (n, p)-proper field ϕ are of this form. Thus theorem 2.1 can be strengthened in this case to the following theorem.

THEOREM 3.1. *Let* F *be a form of degree* p *in* n *variables with a representation* $[\lambda_\alpha, A]$ *in an* (n, p)*-proper field* ϕ, *where* A *is non-singular. The*

matrix A *determines the* λ*'s uniquely, and the* λ*'s determine* A *up to a factor* DJ *on the left.*

The form F is equivalent in ϕ to a form F' with diagonal matrix if and only if F has a minimal representation $[\lambda_\alpha, A]$ where A is non-singular. Then $F' = \lambda_1 x_1^p + \ldots + \lambda_n x_n^p$.

4. *Associated Multilinear Forms.*—With a form $F = a_{ij\ldots m}x_i x_j \ldots x_m$ having a symmetric matrix there is associated a unique multilinear form M_F given by $a_{ij\ldots m}x_i y_j \ldots z_m$ which can be obtained from F by the well-known Aronhold polarization process provided that the field of operations is (n, p)-proper if F is of degree p in n variables. Concerning multilinear forms we have the following theorem.

THEOREM 4.1. *A multilinear form* $M = b_{ij\ldots m}x_i y_j \ldots z_m$ *can be written in a given field as*

$$\sum_{\alpha=1}^{\sigma} L_\alpha M_\alpha \ldots N_\alpha, \tag{4.1}$$

where the L_α *are linear forms in the* x*'s only, the* M_α *are linear forms in the* y*'s only, . . . , and finally the* N_α *are linear in the* z*'s only.*

If $1, 2, \ldots, n$ is the maximum range of the indices $i, j, \ldots, m$ the form M has a representation (4.1) with $\sigma \leqq n^{p-1}$ where p is the number of vectors in the set $(x_i), \ldots, (z_m)$.

The minimum value of σ for which a form M_F can be written as (4.1) in a field ϕ is called the *factorization rank*[1] of F in ϕ. The minimum value of σ for which F can be written as (1.1) is termed the *minimal number* of F. Let $[F]$ now denote the class of forms F defined by the properties

1. The coefficients of F are in a field ϕ, and $(a_{i\ldots m})$ is symmetric.
2. F is of degree p.
3. F involves n variables and cannot be reduced by means of non-singular linear transformations in ϕ to a form with less than n variables.

The minimum value of the factorization ranks of forms in $[F]$ with respect to ϕ is n; this is also true of minimal numbers. Making use of symmetry properties of the matrix $(a_{ij\ldots m})$ of F and rank properties of direct products of 2-way matrices we prove the following theorem which is valid for an (n, p)-proper field.

THEOREM 4.2. *If the minimal number of a form* F *in* [F] *is a minimum for* [F], *the factorization rank of* F *is a minimum for* [F], *and these minimum values are equal; and conversely.*

If the minimum value of the minimal number is taken on for F, the form F is equivalent to a form with diagonal matrix, and M_F is non-singular in the sense of another paper[2] of the author. Conditions for non-singularity of M_F were given in that paper which may hence be applied to F to determine whether or not F is equivalent to a form with diagonal matrix. By

properties of generalized determinants proved elsewhere[3] we have the following theorem.

THEOREM 4.3. *For an* (n, p)*-proper field* ϕ *a form* F *in* [F] *of odd degree is equivalent to a form with diagonal matrix if and only if the generalized determinant*[4] $D = |x_i a_{ij} \ldots_m|$ *signant on* j, . . . , m *factors in* ϕ *into linearly independent linear factors and under reduction in* ϕ *of* D *to* $kx_1 \ldots x_n$ *by non-singular linear transformations,* F *transforms covariantly to a form with diagonal matrix.*

A modification of this theorem holds for forms of even degree. For the complex field the factorability of D into linearly independent linear factors may be recognized with the aid of conditions obtained by Hocevar[5] for the reducibility of a form into linear factors.

We write $F = x_i F_i$, where F is a form in $x_1, \ldots, x_n$. We term $F_1, \ldots, F_n$ the *sub-forms* of F. By rank properties of the associated p-way matrix of F we prove the following theorem.

THEOREM 4.4. *For an* (n, p)*-proper field* ϕ *a form* F *of* [F] *of degree* $p \geqq 3$ *is equivalent to a form with diagonal matrix if and only if the sub-forms of* F *are equivalent in* ϕ *to forms with diagonal matrices.*

If F is of degree $\geqq 3$, and has a representation $[\lambda_\alpha, A]$ where A is non-singular there exist numbers ρ_i in the given field such that $\rho_i F_i$ has a representation $[\lambda_\alpha', A']$ where A' is non-singular. By this property, theorem 4.4, and the fact that the transformations which bring a form of degree $\geqq 3$ with diagonal matrix into a form with diagonal matrix bring any form with diagonal matrix into a like form we prove the following theorem.

THEOREM 4.5. *Let* $F = x_i F_i$. *For an* (n, p)*-proper field* ϕ *a form* F *of the class* [F] *is equivalent to a form with diagonal matrix if and only if the following conditions are satisfied.*

a. *There exist numbers* ρ_i *in* ϕ *such that* $\rho_1 F_1 + \ldots + \rho'' F''$ *has a representation* $[\lambda_\alpha, A]$ *in* ϕ *where* A *is non-singular, and* $\lambda_\alpha \neq 0$ *for each* α.

b. *If condition a is satisfied, assume that* $\rho_1 \neq 0$ *and reduce* $\rho_i F_i$ *by a non-singular linear transformation* T *in* ϕ *to a form* F′ *with diagonal matrix. Let the transformation* T *bring* $F_2, \ldots, F_n$ *into* $F_2', \ldots, F_n'$. *Then* $F_2', \ldots, F_n'$ *are forms with diagonal matrices.*

5. *Ranks and the Minimal Number.*—The values of the factorization rank and minimal number of a form F depend on the given field as can be easily seen by considering binary cubic forms over the real and complex fields. The minimal number and the factorization rank of a form F are invariant under non-singular linear transformations in a given field. Elsewhere[3] the author defined ranks of F and the matrix B associated with F for every grouping of the indices of F into signant partitions, where there are an even number of signant partitions. These ranks were obtained by considering generalized determinant minors of matrices made up of blocks equal to B. It has been proved elsewhere[6] for binary forms and any

field that all ranks with two partitions signant are equal. Simple considerations yield the following theorem concerning the equality of ranks valid for fields for which the matrix of F is unique.

THEOREM 5.1. *The ranks of* F *are equal for a field* ϕ *if and only if the factorization rank and minimal number of* F *with respect to* ϕ *are equal.*

A limited subclass of the class of ranks introduced by the author was defined and studied by Hitchcock.[7] The author extended this class[3] to essentially the largest possible class with the hope that this enlarged class would completely characterize classes of equivalent multilinear forms for arbitrary fields. The class of ranks of a given form contains a finite number of elements. Since the author recently proved[8] that the number of classes of equivalent trilinear forms for non-denumerably infinite fields is non-denumerably infinite, it is impossible to characterize these classes by means of ranks alone; and it is certainly impossible to characterize classes of equivalent ordinary forms by ranks only. It is to be expected that these ranks characterize the classes of equivalent forms for certain finite fields, but this problem has not yet been studied for the general case.

6. *Concluding Remarks.*—By the well-known transition from non-homogeneous polynomials to forms it is evident that many of the theorems [e.g., theorem 1.1] may be stated for ordinary polynomials. The proofs of the remarks and theorems of this paper as well as applications to the problem of factorability of polynomials will appear elsewhere.

[1] Oldenburger, *Bull. Amer. Math. Soc.*, **42**, 871–873 (1936).

[2] Oldenburger, *Trans. Amer. Math. Soc.*, **39**, 422–455 (1936).

[3] Oldenburger, *Ann. Math.*, **35**, 622–657 (1934).

[4] For uses of such determinants involving variables the reader is referred to the following papers:

Oldenburger, *Bull. Amer. Math. Soc.*, **38**, 385–387 (1932).

Oldenburger, *Amer. Jour. Math.*, **59**, 427–435 (1937).

Oldenburger, *Bull. Amer. Math. Soc.*, **43**, 546–553 (1937).

[5] Hocevar, *Compt. Rend.*, **138**, 745–747 (1904).

[6] Oldenburger, *Ann. Math.*, **38**, 172–177 (1938).

[7] Hitchcock, *Jour. Math. and Phys.*, **7**, 40–79 (1927).

[8] Oldenburger, *Duke Math. Jour.*, **2**, 671–680 (1936).

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